

Comparative studies on the functional morphology of two gekkonid lizards¹

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(With two plates)

SUMMARY

The fine morphology of adhesive bristles in the gekkonids *Tarentola mauritanica* and *Hemidactylus frenatus* was studied by means of scanning electron microscopy (SEM). The adhesive apparatus is similar in both species, and so is their adhesion ability. Former theories regarding gekkonid "strolling on the ceiling" (e.g. insertion of claws, use of suckers, electrostatic forces) are dealt with and are disproved. A single seta of the foot pads consists of a shaft, the surface of which shows longitudinal structures terminally ramifying into first, second or third branchings. These branchings form terminal layers, sometimes with deepenings on the end of each ultimate branch, where adhesion proper occurs.

Adhesion is a physical process relying on the surface tension of the substratum and can be precisely measured by means of the contact angle between distilled water and the substratum. Various materials possess different surface tensions which can even be altered, e.g. by coronary discharge. Increasing surface tensions offer increasing clinging abilities of the geckos.

INTRODUCTION

After the functional morphology of adhesive toes has been elucidated in the Mediterranean gekkonid lizard *Tarentola mauritanica* (Hiller 1968) it is now possible to extend these findings to other gekkonids. The present paper offers an explanation of the adhesive abilities of *Hemidactylus frenatus*, in comparison with *Tarentola mauritanica*. In both lizards body size, toe morphology and adhesive function are similar.

The gecko's ability of walking on vertical surfaces and even on ceilings has been known since a long time. Various authors have speculated on it, and several theories have been advanced. Thus, Cartier (1872) disproved a secretory adhesion (as in tree frogs) because of the lack of digital glands. Tornier (1889) favoured the theory of suction, and Haase (1900) and Schmidt (1904) thought that electrical forces would be responsible for adhesion. Mahendra (1941) arrived at the conclusion that geckos would use their digital setae as claws inserting them into the substratum. The first experimental studies of the problem were done by Hora (1923), who offered substrata of various surface structures correlating them to climbing ability. Dellit (1949) did away with the theory of suction by reducing air pressure down to 0.5 mm Hg,

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and yet fresh killed geckos would still cling to the surface structures in the same manner as before. In addition, Dellit could also disprove Schmidt's (1904) theory of electrostatic adhesion by employing X-rays on a gecko clinging to a vertical metal surface. Yet, clinging ability was not reduced. Then, Dellit tried to clean glass surfaces with petrol, and promptly the geckos fell off these substrata. Hence, Dellit concluded that climbing geckos would grip "into" the minute rugosities of the surface. His microscopic study of the adhesive bristles led him to the above mentioned conclusion. However, light microscopy could only partly reveal the fine structure of the setae. His "cleaning" of the glass plates with petrol left a thin film of long-chained carbohydrates, and thus his conclusions were not too well founded. Haase's (1900) adhesion theory was not disproved either.

Obviously, the problem could only be solved by an improved observation technique, functionally and microscopically. Using electron microscopical methods, Altevogt (1954) could show that there are very many more setal ramifications beyond those known to light microscopists. Later, Ruibal & Ernst (1965) continued such studies by transmission electron microscope and depicted the terminal branchings of the digital bristles.

MATERIALS AND SCANNING ELECTRON MICROSCOPICAL (SEM) METHODS

Toes of *Tarentola mauritanica* and *Hemidactylus frenatus*,³ the Indian house gecko were studied by using the "Stereoscan" Mk 1

and Leitz-AMR 1000.⁴ Both these instruments yield images of the surface structures with very high depth of focus. The objects to be studied are glued to aluminium stages by liquid contact silver dispersion. Then they are coated with gold and carbon in alternating repetition.⁵ The study proper is done under 20 kV accelerating voltage.

RESULTS

Morphology of adhesive setae

a) *Tarentola mauritanica*

The survey (fig. 1) shows that the adhesive pads cover each toe totally in an imbricate manner. The distal parts of the setae are curved towards a proximal direction. Proximally, their diameter is about 2.5 μm . Their distal ramifications end in plate-like structures of 0.5 μm with a slight central deepening (fig. 2). The surfaces of these minute ramifications are normally arranged in one level at right angles to the longitudinal axis of the seta. The setae originate in fours from a papilla of the basal fibrous layer (Hiller 1972). The distal surfaces, the site of adhesion, of each four setae are also arranged in one level. This is an important fact to make adhesion at all possible.

The distal ramifications can be traced down along the shaft of each seta right to its base. Hence, column-like cannelures can be seen (fig. 3). They are proof of their ontogenetic development as epidermal structures, which also explains the occasional occurrence of other surface structures along the setal shaft without any relevance to adhesion.

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b) **Hemidactylus frenatus**

A palmar view of *Hemidactylus frenatus* shows a typical arrangement of adhesive pads along the toes (fig. 4). Only the distal pad is not paired, the others being arranged in pairs under an angle of about 70° to the median line. The latter is a deep epidermal groove (fig. 5) with several irregular interruptions, and sometimes this medial groove is even absent. The adhesive bristles are 4.5 μm wide, and their length depends on their position on each pad. On the proximal side of a pad they are 50 μm long (fig. 6), and their length increases by about 50 per cent in a distal position (fig. 7). The setae originate in twos to fours as in *Tarentola*. Sometimes, even a single seta sprouts from one papilla. These papillae also give rise to minute and simple setae of only 2 μm length (fig. 8).

Along the shaft of the adhesive setae one can sometimes trace the ramification, so fully developed at the distal portion. Ramification proper begins about 10-15 μm from the distal surface, and sometimes even 5 μm will do. Besides this primary ramification there are secondary branchings yielding even more adhesive surfaces. The length of these secondary ramifications ranges from 2-5 μm (fig. 9). The diameter of these final branches is 0.2 μm. All setae are again curved proximally. There is hardly a broadening of the terminal surfaces in this species.

COMPARISON OF ADHESIVE STRUCTURES IN
Tarentola AND *Hemidactylus*

The gross morphology in *Tarentola* reveals adhesive pads without interruption across the whole toe. All setae are uniformly curved proximally. In *Hemidactylus*, however, the pads are separated by a medial groove, and consequently there is the 70° position refer-

red to above. While there are almost no differences in the structure of the setal shaft in both species, the terminal ramifications are quite different. In *Tarentola*, there are three levels of branchings, in *Hemidactylus* but two. It is highly interesting and certainly very important for the process of clinging that the width of the terminal bristles is 0.2 μm in both lizards. This finding holds also for the New World Iguanids *Anolis carolinensis* and *Anolis roquet extremus* (Hiller 1968). The terminal curvature of setal ramification is equal in both, *Tarentola mauritanica* and *Hemidactylus frenatus*.

Judging from the fine morphology of bristles in *Tarentola* and *Hemidactylus* one may rightly infer that the formation of adhesive structures (Hiller 1970, 1972) is similar if not equal. According to these findings, the setal ramifications originate first by a growth process of keratine bundles from the Oberhäutchen—cell (Oz) into cells of the so called clear layer (Hs). Hence, a matrix of adhesive bristles is formed, and subsequently Hs- and Oz-layer separate from each other giving rise to the adhesive apparatus proper. In the following shedding, the Hs-layer is removed, and the newly formed adhesive bristles are ready for immediate function.

FUNCTIONING OF ADHESIVE BRISTLES

Judging from the almost identical morphology of adhesive setae in both gekkonids there can be no doubt about the functional principle (Hiller 1968), all the more as *Hemidactylus* is almost as good a climber as *Tarentola*. Though this—physical—principle has been fully elucidated (Hiller 1968), the old theories of suction etc. are still relied on in several scientific and popular papers on this astonishing gekkonid ability (for instance

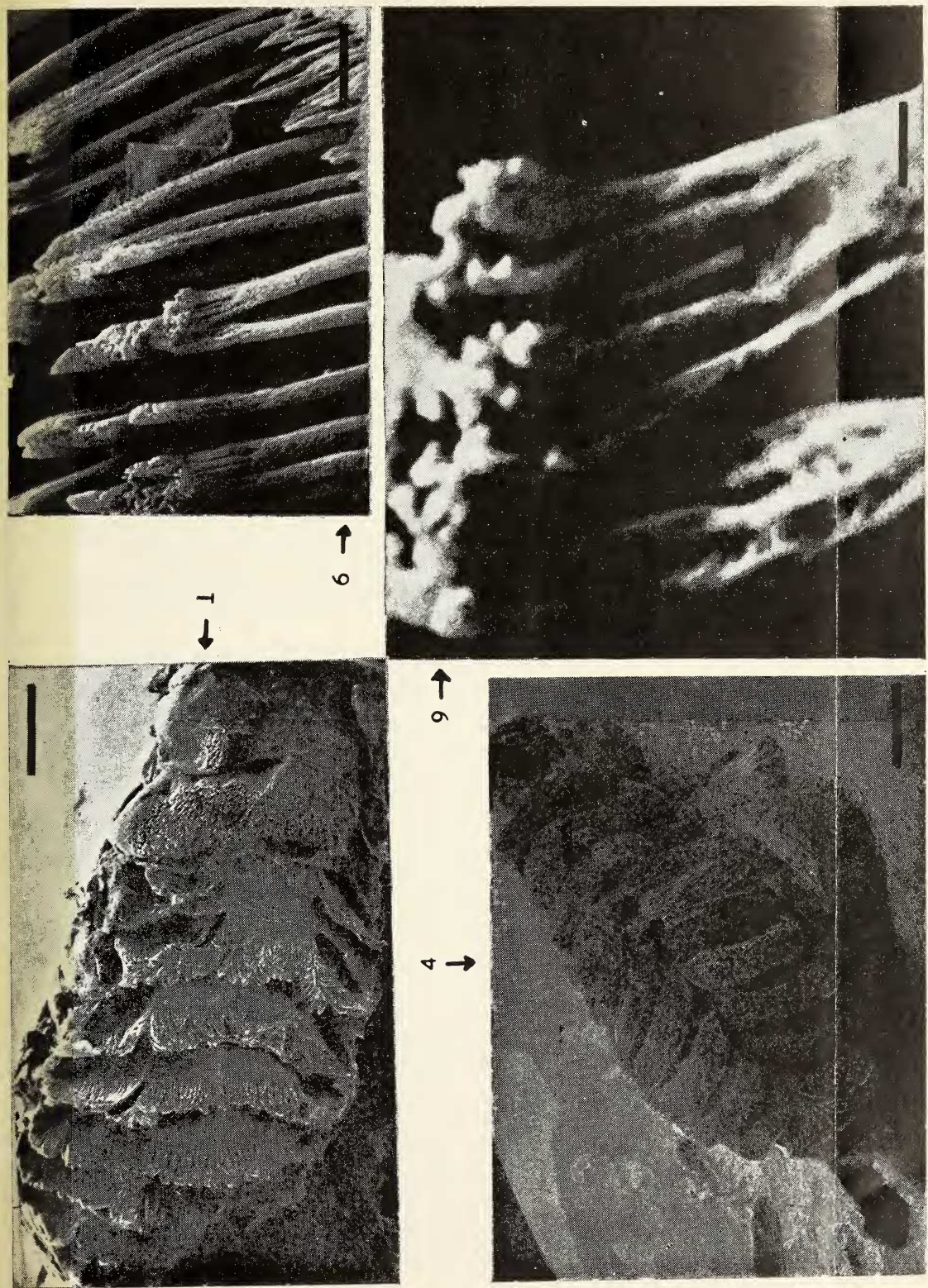


Fig. 1. *Tarentola mauritanica*, toe showing the adhesive pads. Scale 400 μm . Fig. 2. *Hemidactylus frenatus*, palmar view of toe. Note the typical arrangement of adhesive pads. Scale 400 μm . Fig. 3. *Hemidactylus frenatus*, proximal side of a pad with 50 μm long setae. Scale 10 μm . Fig. 4. *Hemidactylus frenatus*, distal ends of a seta, showing the first and second grade ramifications. Scale 1 μm .

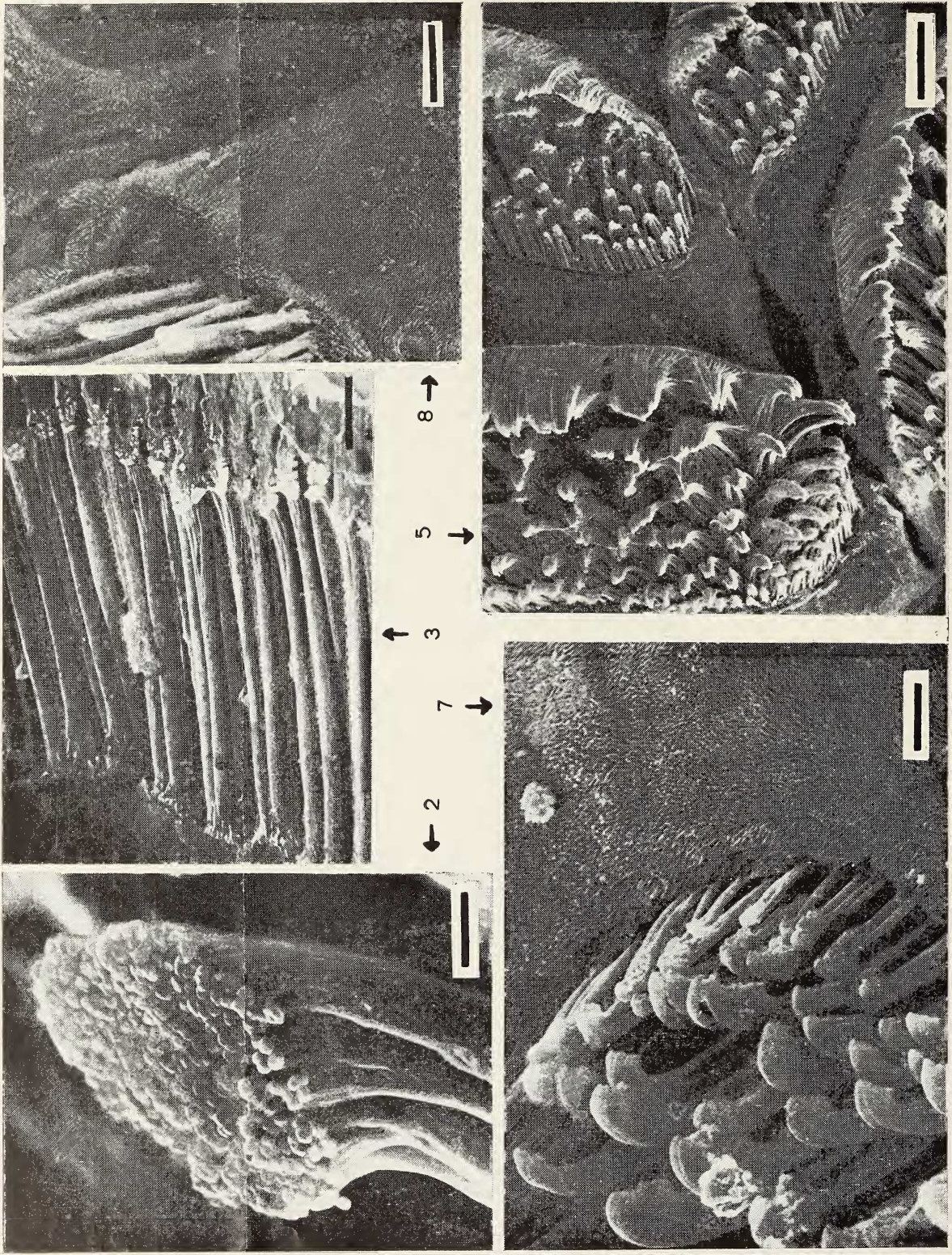


Fig. 2. *Tarentola mauritanica*, distal ramification of a seta. Scale 1 μm. Fig. 3. *Tarentola mauritanica*, adhesive seta showing column-like cannelures along the shaft. Scale 15 μm. Fig. 4. *Hemidactylus frenatus*, median epidermal groove between the adhesive pads. Scale 40 μm. Fig. 5. *Hemidactylus frenatus*, adhesive bristles in a distal position (left) increases by about 50 per cent. Scale 20 μm. Fig. 6. *Hemidactylus frenatus*, numerous minute and simple setae of only 2 μm length cover the region between the footpads. Scale 20 μm.